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Fruiting phenology and implications of fruit availability in the fragmented Ngele Forest Complex, KwaZulu-Natal, South Africa

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ABSTRACT

Fragmented forests are under threat worldwide. Understanding fruiting phenology of these is important in terms of food supply to frugivores, particularly avifauna, which can move varying distances between forest fragments. Fragmentation can affect tree species' diversity, which in turn determines fruit availability and quality. Many forest types have predictable, synchronous fruiting which is often linked to climatic cues. However, some forest types show no seasonality in fruiting and have varying fruit outputs between years. We investigated the fruiting phenology of four forest fragments in the Ngele Mistbelt Forest complex, which forms part of the Eastern Mistbelt Forests in KwaZulu-Natal, using fruit-fall traps. We hypothesized that fruit availability would vary with forest fragment size and with season. Fruiting in three of the forest fragments did not show seasonal fruiting trends and had increased fruiting in late summer and autumn months. Middlebrook showed trends. Fruiting varied significantly between months for all fragments, and where annual variation was observed trends were insignificant. The number of fruiting species per fragment varied significantly and numbers of fruiting species per fragment per month were generally low. Tree species varied in their fruiting patterns between fragments and fruiting of *Afrocarpus*/*Podocarpus* trees and the implications for endemic, endangered Cape Parrots are discussed as an example. In summary, these forests have variable and unpredictable fruiting between fragments. These results highlight the need to conserve forest fragments of varying sizes as a network to provide a year round supply of fruits to frugivores.

1. Introduction

Forests make up approximately one third of the worlds land cover (FAO, 2010). Globally, South America and Africa currently account for the greatest levels of deforestation (FAO, 2010), a process that affects both habitat quality and species diversity (Wade et al., 2003). It is well established that human-induced changes, such as fragmentation, in forest ecosystems affect the health and the viability of forest fragments and their associated fauna, particularly species which depend on mature, interior forest areas (Jamoneau et al., 2012; Lawes, 1990; Means, 2010; Restrepo et al., 1999; Symes and Downs, 2002; Wethered and Lawes, 2003). The forest biome is the smallest of the eight biomes in South Africa (Mucina and Geldenhuys, 2006; Rutherford and Westfall, 1986) and the KwaZulu-Natal province contains one sixth of South Africa's forests (Low and Rebelo, 1996; Mucina and Geldenhuys, 2006). These forests are historically fragmented due to fire caused by lightning and humans during the late Holocene, and climate change (Lawes, 1990). Following this, past timber exploitation, particularly of straight stemmed *Podocarpus* trees (Lawes et al., 2007; Wirminghaus et al., 1999) is believed to have negatively affected forest fragments of this afromontane complex (Cooper, 1985; Moll, 1972). Eastern Mistbelt Forests, which form part of the Southern Mistbelt Forest Group, are naturally fragmented forests which occur from the Eastern Cape to KwaZulu-Natal (Cooper, 1985; Low and Rebelo, 1996; Mucina and Geldenhuys, 2006; Von Maltitz et al., 2003) and are dominated by *Afrocarpus*/*Podocarpus* species (yellowwoods) (Moll, 1972; Pooley, 1993). Among these is *Podocarpus henkelii*, a near endemic species for this habitat type (Mucina and Geldenhuys, 2006).

Commercial plantation practices have replaced much of the surrounding grasslands (Cooper, 1985; Lawes et al., 2004; Mucina and Geldenhuys, 2006) and have disingenuously improved the connectivity between forest fragments (Gascon et al., 1999; Wethered and Lawes, 2003). This is because matrix habitats which are more similar to the remaining forest fragment can facilitate movement of certain species between fragments (Herrera and García, 2009; Tewksbury et al., 2002). Forest fragments provide both permanent habitats for resident species (insectivores and forest generalists), as well as temporary foraging sites for species which move between them (Neuschulz et al., 2013). Connectivity between forest fragments is important for frugivores as these are affected by fragment food production (Lawes et al., 2004; Symes et al., 2002; Wethered and Lawes, 2003) and various forest fragments could provide food sources at times of fruit scarcity (Haugaasen and Peres, 2005). Despite fragmentation, studies in South Africa have

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shown that large frugivorous species and forest specialists move between forest fragments to forage (Lenz et al., 2011; Neuschulz et al., 2013). However, long distances between fragments could impede smaller avian frugivores, as well as mammalian species, which have also been shown to track fruiting trees (e.g. Davis et al., 2006). Should connectivity between fragments be lost, other important processes, such as seed dispersal, could also be lost (Cordeiro and Howe, 2003; Galanes and Thomlinson, 2009; Lehouck et al., 2009).

Phenological cycles of trees are established in order to maximize reproductive success (Anderson et al., 2005). Several factors have been shown to influence fruiting phenology, including: phylogeny, environmental conditions, and biogeographic history (Griffiths and Lawes, 2006; Marco and Paez, 2002). In areas where there are strong annual climatic cues, phenology is mostly predictable (Haugaasen and Peres, 2005). This is generally true for temperate forests which respond to rainfall and temperature changes; however some tropical forests respond similarly (Anderson et al., 2005; Haugaasen and Peres, 2005; Hilty, 1980; Lieberman, 1982). Where forests are constantly 'wet', cues such as day length and temperature can influence, but do not limit, fruit production (Morellato et al., 2000). Furthermore, climatic influences can act differently on various tree species (Chapman et al., 2005).

We selected the Cape Parrot (*Poicephalus robustus*) as an example to consider the implications of fruit availability and connectivity between forest fragments in the Ngele Forest complex, particularly with regards to their preferred *Afrocarpus*/*Podocarpus* kernel fruits (Skead, 1964; Wirminghaus et al., 2002). The Cape Parrot is both endemic and one of South Africa's most endangered birds (Downs, 2000, 2005 Perrin, 2005 Wirminghaus et al., 1999, 2000). It is also a comparatively well studied species within the Eastern Mistbelt Forests. Cape Parrot population declines have been linked with the loss of *Afrocarpus*/*Podocarpus* trees (among other reasons), particularly *Afrocarpus falcatus*, which are the preferred nesting and socializing sites (Wirminghaus et al., 2001a, 2001b). These parrots feed on a range of indigenous and exotic tree species which produce fruits with kernels, discarding most of the fruit flesh (Wirminghaus et al., 2002). They are particularly specialized in feeding on *Afrocarpus*/*Podocarpus* fruits when these are available, and in times of food scarcity have been observed to feed on commercial orchards (Downs, 2005; Symes and Downs, 2002; Wirminghaus et al., 2002). This species has a wide ranging nomadic feeding behavior (Downs, 2005; Skead, 1964; Wirminghaus et al., 2001a) and the availability of these fruits has been shown to influence their movement patterns (Wirminghaus et al., 2000). Consequently, the variation in fruit production has important implications for forest frugivore species, which are particularly reliant on species which fruit during times of fruit scarcity (Anderson et al., 2005).

The primary aim of this study was to describe the fruiting phenology, based on all fruits caught in fruit-fall traps, of four forest fragments from the Ngele Eastern Mistbelt Forest Complex. We hypothesized that fruiting would vary seasonally and between forest fragments of differing size. We predicted that fruit availability, in terms of diversity of fruiting species, would be lower in smaller fragments. This would have important implications for the conservation of these fragments as a whole, particularly for specialist species such as the Cape Parrot.

2. Materials and methods

Four different forest fragments namely: Mackton, Middlebrook, Ngele and Ntunta, were selected in the Weza district (30° 32′ 22″S, 29° 40′ 32″E) in KwaZulu-Natal, South Africa (Fig. 1). Peak precipitation occurs during the spring–summer period with an average annual rainfall of 1000 mm (Mucina and Geldenhuys, 2006). Additionally, heavy summer mists occur in these forests (Von Maltitz et al., 2003). Geologically, the soils for these forests are predominantly Dolerite based (Norman, 2012; Von Maltitz et al., 2003). Mackton and Middlebrook were considerably rockier with steeper slopes.

Fruit traps were randomly erected in each forest fragment and were suspended at least 10 m apart; however this spacing was dependent on the availability of suitable trees from which to suspend the trap, the topography of the area, and the size and shape of the forest fragment (Table 1). Fruit traps were constructed by suspending a 1 m × 1 m square of 70% shade cloth approximately 1 m above the ground. A weight was placed in the center of the trap to ensure that all objects falling on the trap would roll towards the center and thus be retained. Numbers of fruit traps per forest fragment are detailed in Table 1. Trap falls were collected monthly from February 2010 to February 2012. Fruits and parts of fruits were kept in paper bags and the remaining debris were discarded. Fruits and parts of fruits were then identified and counted. Where fruits or fruit segments could not be identified, seeds from these fruits were planted to facilitate identification. Classification of taxa follows that of Raimondo et al. (2009) and species collected are listed in Table 2. Specimens were taken for comparison against reference material in the H. Nicholson/T. Abbott herbarium located in the Umtamvuna Nature Reserve, and where necessary, material was referred to the curator for verification.

To determine if the number of fruiting species differed between months and whether the number of fruiting species differed between fragments a one-way analysis of variance (ANOVA) was run. Where significant differences were detected, *post-hoc* Tukey tests were run. A dependent sample t-test was used to determine if there was a difference in the number of fruiting species per year in each forest fragment. All analyses were run using Statistica (Statsoft, Version 7, Tulsa, OK, USA).

3. Results

Fruits present in the trap were from several sources including: large and small trees, creepers and lianas, wind-blown fruits from trees outside the plot, trees whose canopy sections overlap the plots, and fruits transported and dropped by birds and animals. Fruiting species composition based on trap collections differed between the four forest fragments (Table 2). Fruit from a total of 78 species were collected from the four forest fragments (Table 2). Results are expressed as percentages of this total species number. Nearly half of the species were found in only one forest fragment, while approximately 18% of species were either found in all fragments, three fragments or two fragments only (Table 2).

The percentage of trees fruiting in Middlebrook showed seasonality, while no seasonal trends were observed in the remaining forest fragments. At the Middlebrook site, fewer fruit were collected in the traps in the warmer months (November–March) than in the colder months (May–August) (Fig. 2). Ntunta and Mackton showed the opposite trend, in that the number of species in fruit increased in warmer months and decreased from August–September (Fig. 2). The total number of fruiting species collected in traps in each fragment differed significantly between months (ANOVA $F_{25, 75} = 1.988$, $P = 0.013$). December 2010 had significantly less fruit than June 2011 (*post-hoc* Tukey, $P = 0.031$, Fig. 2). Higher percentages of fruiting species were observed in Mackton and Middlebrook in the second year of sampling, while these remained relatively constant between years in the larger fragments (Fig. 2). However, fruiting between years did not differ for any of the forest fragments sampled (Mackton: $t_{11} = 2.195$, $P = 0.051$; Middlebrook: $t_{11} = 1.532$, $P = 0.154$; Ngele: $t_{11} = 0.779$, $P = 0.452$; Ntunta: $t_{11} = 0.542$, $P = 0.599$). While Ngele was the largest forest fragment sampled, the total number of fruiting species recorded was similar to the smallest forest fragment (Table 1).

In general, the percentage of fruiting species ranged between c. 10 and 35% of the possible total of 78 species for all forest fragments (Fig. 2). For all forest fragments the percentage of the total number of species fruiting was always below 50% for each month sampled (Fig. 2). The number of fruiting species was also significantly different between forest fragments (ANOVA $F_{3, 96} = 8.71$, $P < 0.05$), with Ntunta having significantly more fruiting species per month (11.2 ± 0.55,

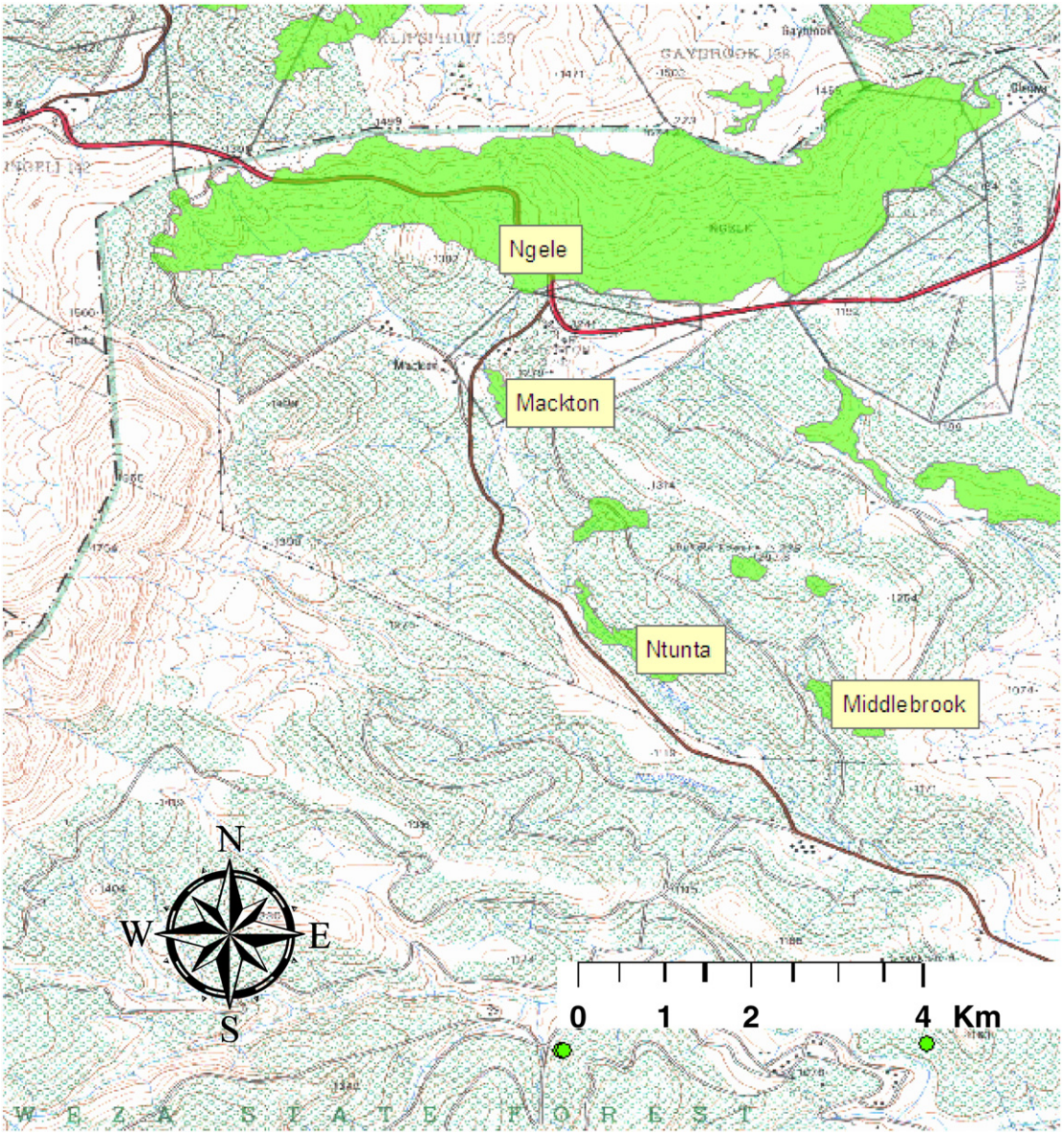

Fig. 1. Map of the four forest fragments from the afromontane forest complex sampled in this study.

mean ± SE) than Mackton (8 ± 0.52) and Middlebrook (8 ± 0.58) (*post-hoc* Tukey, $P < 0.05$, Fig. 2). Ngele had an average of 9.44 ± 0.40 species fruiting per month.

Fruits were usually present in very few of the traps in each forest fragment, with most fruit species recorded in less than 20% of the traps (Fig. 3). Differences were observed in the fruiting periods of species between fragments. It was observed that in some forest fragments certain species would fruit for several months while in other fragments these same species would only fruit for a few months (Fig. 4). *Celtis africana* was present in all fragments and fruited nearly year round, except in Middlebrook (Fig. 4). In general, fruit trap data showed that forest fragments varied in the species which contributed to the most fruiting months. These species fruited almost year round in specific fragments, but had very low fruiting or were absent in the remaining fragments. Some examples include: *Ptaeroxylon obliquum* with 23 months fruiting in Mackton; *Cryptocarya woodii* with 19 months in Middlebrook; *Monanthotaxis caffra* with 24 months in Ntunta; and *P. henkelii* with 23 months in Ngele (Fig. 4). In Mackton a shrub species, *Hyperacanthus amoenus*, fruited for 19 months, but was absent from the other forest fragments. Similarly, a vine species, *Combretum edwardsii*, fruited year round in Ngele, but had low fruiting or was absent in the remaining fragments (Fig. 4).

Variability in fruiting was further highlighted by the difference in trends observed for *Afrocarpus*/*Podocarpus* species. The trees of *A. falcatus* and *Podocarpus latifolius* occurred in all forest fragments of this study, while *P. henkelii* only occurred in Mackton and Ngele. Fruits from all three observed *Afrocarpus*/*Podocarpus* species were only collected in the largest fragment, Ngele. *P. henkelii* fruits were absent

Table 1
Size and location of each forest fragment and the respective number of fruiting species and fruit traps in each plot for the duration of the study from February 2010 to February 2012.

Forest fragment	Grid reference	Fragment area (ha)	Altitude (m a.s.l.)	No. of fruit traps	Total no. of fruiting species
Mackton	30° 32′ 26″S 29° 41′ 02″E	10.8	1300	20	34
Middlebrook	30° 34′ 10″S 29° 42′ 38″E	14.6	1164	20	46
Ngele	30° 32′ 22″S 29° 40′ 32″E	710.0	1324	26	36
Ntunta	30° 33′ 51″S 29° 41′ 24″E	22.3	1100	24	45

Table 2
Plants species identified from fruit trap samples, where '1' indicates presence of fruit in a forest fragment and the species number corresponds to Figs. 2 and 3.

Species number	Family name	Species name	Forest fragment			
			Mackton	Middlebrook	Ngele	Ntunta
1	Acanthaceae	*Thunbergia alata*		1		
2	Anacardiaceae	*Harpephyllum caffrum*		1		1
3	Anacardiceae	*Protorhus longifolia*		1		1
4	Annonaceae	*Monanthotaxis caffra*	1	1	1	1
5	Apocynaceae	*Carissa bispinosa*				1
6	Apocynaceae	*Secamone* sp.	1	1	1	1
7	Apocynaceae	*Strophanthus speciosus*	1	1		1
8	Aquifoliaceae	*Ilex mitis*				1
9	Araliaceae	*Cussonia sphaerocephala*		1	1	1
10	Araliaceae	*Cussonia spicata*	1			
11	Araliaceae	*Schefflera umbellifera*	1			1
12	Asparagaceae	*Asparagus setaceus*		1		
13	Asteraceae	*Senecio helminthoides*	1			
14	Capparaceae	*Capparis tomentosa*		1		
15	Celastraceae	*Allocasine laurifolia*		1		
16	Celastraceae	*Gymnosporia harveyana*	1	1		1
17	Celastraceae	*Gymnosporia nemorosa*			1	
18	Celastraceae	*Hippocratea schlechteri*			1	
19	Celastraceae	*Maytenus peduncularis*	1	1		
20	Celastraceae	*Pleurostylia capensis*		1		1
21	Celastraceae	*Pterocelastrus rostratus*				1
22	Celastraceae	*Putterlickia verrucosa*				1
23	Celastraceae	*Elaeodendron croceum*				1
24	Celtidaceae	*Celtis africana*	1	1	1	1
25	Combretaceae	*Combretum edwardsii*	1		1	1
26	Combretaceae	*Combretum kraussii*	1	1	1	1
27	Connaraceae	*Cnestis polyphylla*				1
28	Cornaceae	*Curtisia dentata*			1	
29	Cucurbitaceae	*Coccinia hirtella*		1		
30	Dioscoraceae	*Dioscorea continfolia*		1		
31	Ebenaceae	*Diospyros villosa*		1		
32	Ebenaceae	*Diospyros whyteana*	1		1	1
33	Ebenaceae	*Euclea crispa*		1		
34	Fabaceae	*Dalbergia obovata*		1		
35	Flacourtiaceae	*Kiggelaria africana*	1		1	1
36	Flacourtiaceae	*Scolopia mundii*	1	1	1	1
37	Flacourtiaceae	*Trimeria grandifolia*	1			
38	Hamamelidaceae	*Trichocladus ellipticus*	1	1	1	1
39	Lauraceae	*Cryptocaria woodii*	1	1	1	1
40	Lauraceae	*Occotea bullata*		1	1	1
41	Luzuriagaceae	*Behnia reticulata*	1			
42	Malvaceae	*Grewia lasiocarpa*	1	1		1
43	Malvaceae	*Grewia occidentalis*		1		
44	Meliaceae	*Ekebergia capensis*	1	1	1	1
45	Melianthaceae	*Bersama tysoniana*		1		
46	Monimiaceae	*Xymalos monospora*		1	1	1
47	Moraceae	*Ficus craterostoma*				1
48	Myrsinaceae	*Rapanea melanophloeos*	1	1	1	1
49	Myrtaceae	*Eugenia natalitia*			1	
50	Myrtaceae	*Eugenia zuluensis*	1	1		
51	Myrtaceae	*Syzigium gerardii*		1	1	1
52	Phytolaccaceae	*Phytolacca octandra*	1			
53	Podocarpaceae	*Podocarpus falcatus*	1		1	1
54	Podocarpaceae	*Podocarpus henkelii*			1	
55	Podocarpaceae	*Podocarpus latifolius*	1	1	1	1
56	Ptaeroxylaceae	*Ptaeroxylon obliquum*	1	1	1	1
57	Rhamnaceae	*Helinus integrifolius*	1	1	1	
58	Rhamnaceae	*Scutia myrtina*			1	
59	Rosaceae	*Prunus africana*			1	1
60	Rubiaceae	*Burchelia bubalina*				1
61	Rubiaceae	*Canthium inerme*		1		
62	Rubiaceae	*Canthium mundianum*	1	1	1	1
63	Rubiaceae	*Homalium dentatum*				1
64	Rubiaceae	*Hyperacanthus amoenus*	1			
65	Rubiaceae	*Psychotria capensis*				1
66	Rubiaceae	*Rothmannia capensis*	1	1	1	1
67	Rubiaceae	*Rothmannia globosa*			1	1
68	Rutaceae	*Calodendrum capense*			1	
69	*Rutaceae*	*Clausena anisata*	1	1	1	
70	Rutaceae	*Vepris lanceolata*		1	1	
71	Rutaceae	*Zanthoxylum davyi*			1	
72	Sapotaceae	*Mimusops obovata*		1		1
73	Scrophulariaceae	*Halleria lucida*	1	1	1	1
74	Sterculiaceae	*Dombeya burgessiae*		1		1
75	Thymelaeaceae	*Dais cotinifolia*		1		
76	Thymelaeaceae	*Peddiea africana*	1	1		
77	Vitaceae	*Rhoicissus rhomboidea*		1		1
78	Vitaceae	*Rhoicissus tomentosa*	1		1	1

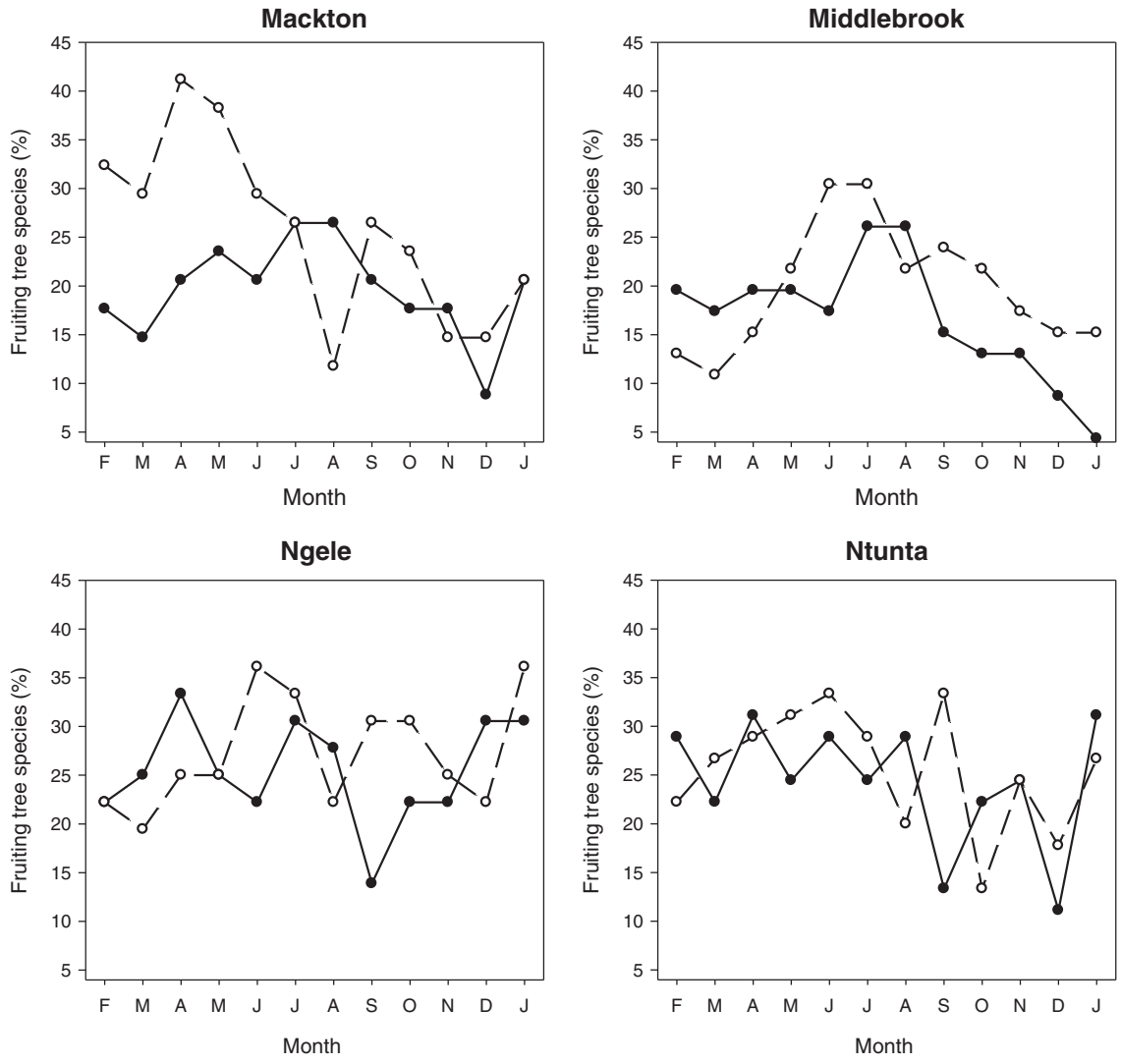

Fig. 2. Percentage of the total number of fruiting species collected in all forest fragments in this study that are present in each forest fragment for the period February 2010–January 2011 (—●—) and February 2011–January 2012 (- -○- -).

from Mackton and *A. falcatus* fruits were not collected in Middlebrook (Fig. 5), despite trees being recorded there previously. Of the podocarps, *P. henkelii* produced the most fruit, almost consistently throughout the year, particularly in the Ngele forest fragment (Fig. 5). *Afrocarpus*/*Podocarpus* fruit production was lower in all other fragments, especially in the two smallest fragments, Mackton and Middlebrook, where asynchronous fruiting between species was only observed in four of the possible 25 months sampled, with predominantly less than 10% of fruit collected in all traps (Fig. 5). There was also no overlap in months of fruiting between these two small fragments (Fig. 5). *Afrocarpus*/*Podocarpus* species were in fruit for 24 of the 26 months observed at both Ngele and Ntunta. No two fruiting months overlapped for this species and fruiting proportions and occurrences remained low (Fig. 5).

4. Discussion

Predictable fruiting phenology is most often linked with climatic cues, and seasonal fruiting patterns have been highlighted around the world, for example: subtropical broad-leaved forests of China (Du et al., 2009), the tropics in Côte d'Ivoire (Anderson et al., 2005), lowland tropical rainforests in central Gabon (White, 1994), Bolivian dry forests (Justiniano and Fredericksen, 2000), Australian temperate wet sclerophyll forests (French, 1992), and tropical montane cloud forests in Mexico (Williams-Linera, 2003). While a phenological study on a South African coastal forest also showed seasonal trends (Bleher et al., 2003), this was not the case for the forest fragments of this study. In the current study, with the exception of Middlebrook (which showed a seasonal fruiting pattern), the fruiting patterns observed in Ntunta and Mackton were not seasonal. Fruit availability was generally higher from late summer through autumn. The largest forest fragment, Ngele, also showed no seasonal trend in fruit availability. A study that used field guide information and only the 30 most abundant tree species, found that Ngele forest had greater fruiting in summer than in winter (Griffiths and Lawes, 2006). This contrasts results from a field study which indicated that Ngele had the greatest number of fruiting species in winter (Wirminghaus et al., 2001c). While trends from our study were similar for Ngele to Griffiths and Lawes (2006), the number of species fruiting per month was higher in their study. Contrastingly, in a subtropical coastal dry forest in South Africa fruiting peaks were observed during colder months (Bleher et al., 2003), which was true for Middlebrook and on a few instances in the other forest fragments.

Fruiting varied significantly between months for all fragments, and while the smaller fragments showed variation in fruiting between years, this was not significant. Such differences could be attributed to the absence of some species in various forest fragments. In some cases species were present but did not fruit. Differences in monthly fruiting in Ngele forest have been previously observed (Wirminghaus et al., 2001c). Variations in fruiting period, synchronicity and duration

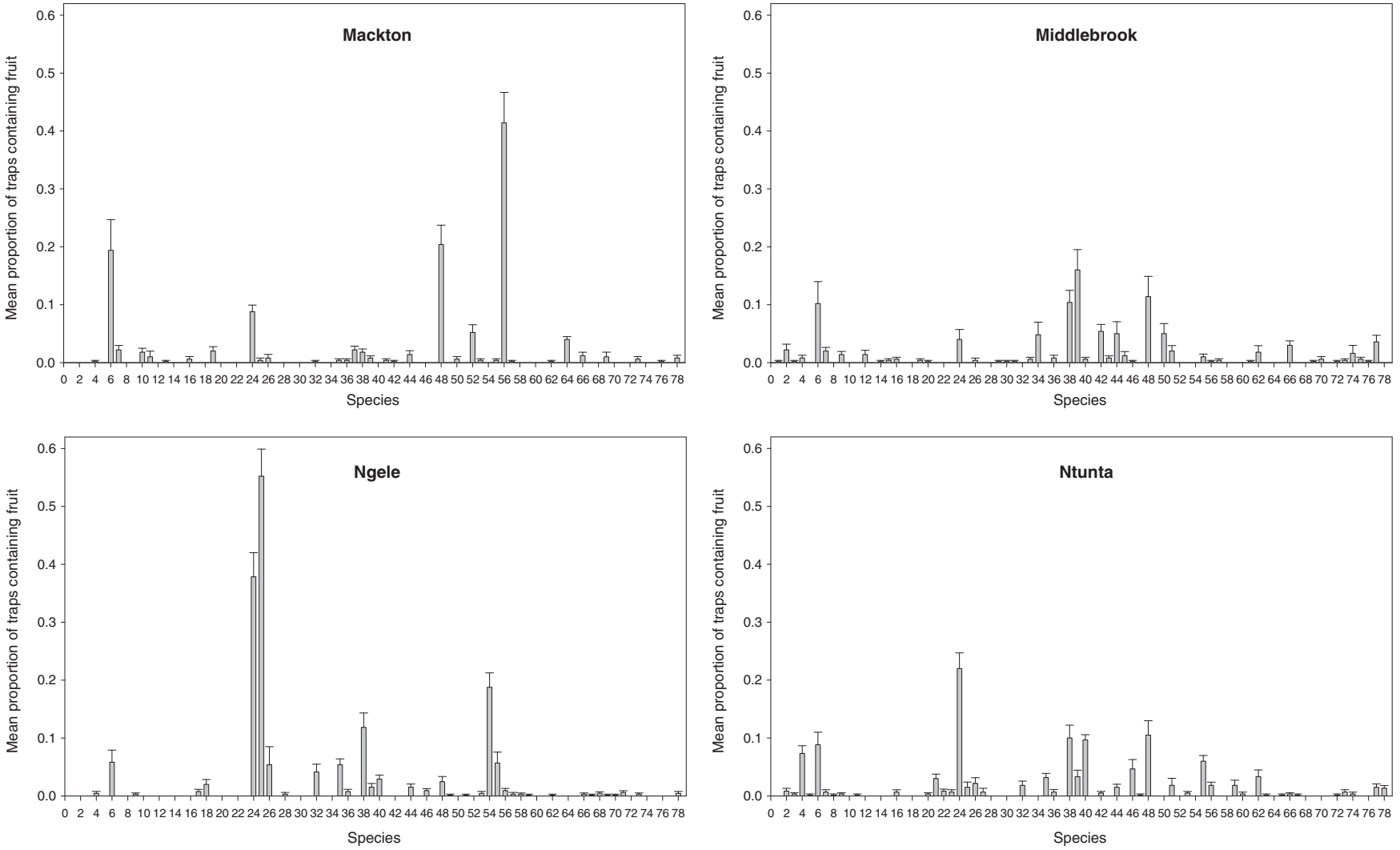

Fig. 3. Proportion of traps containing the respective fruiting species in each forest fragment for the period February 2010 (month 1) to February 2012 (month 25).

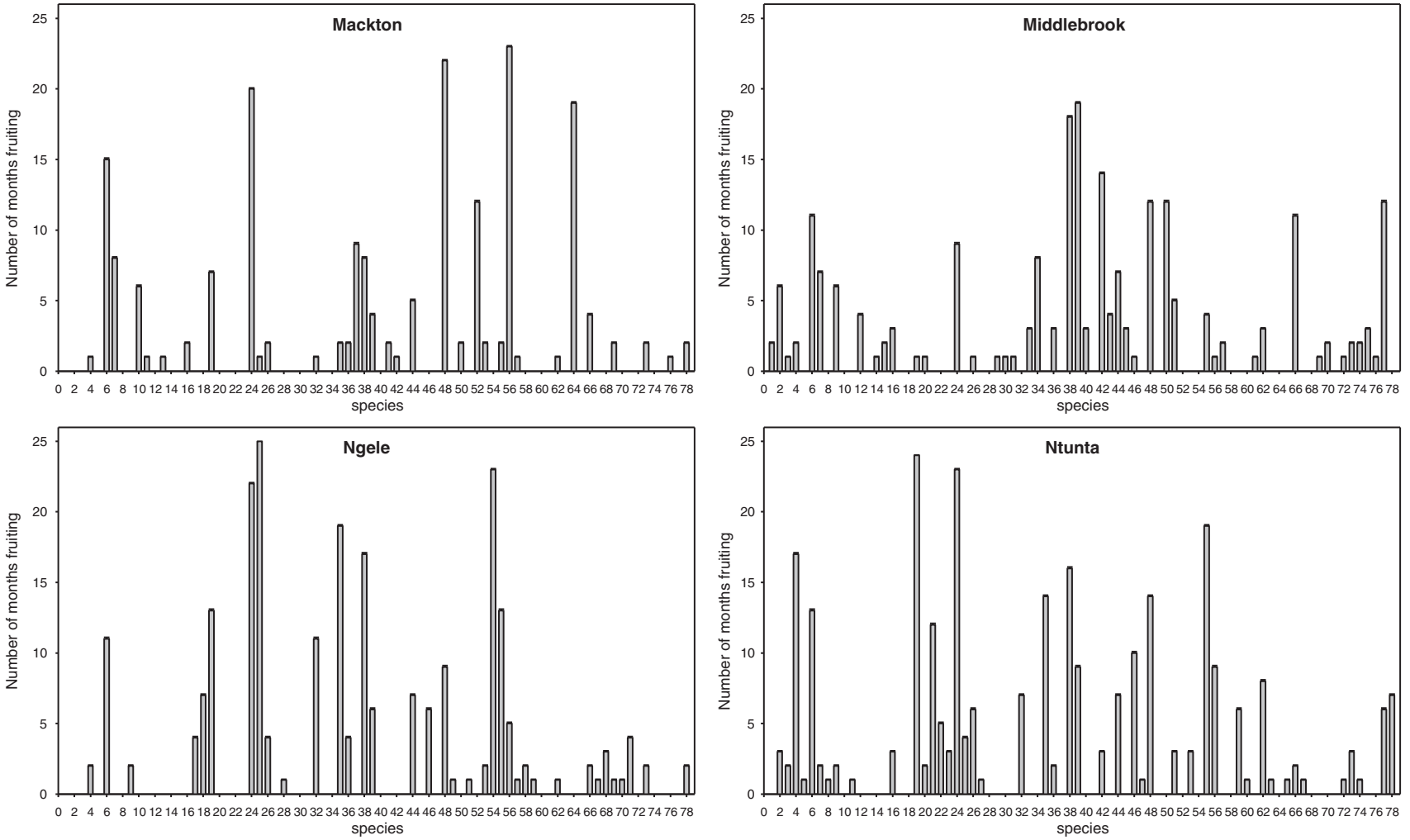

Fig. 4. Number of fruiting months for each species over a two year period in each forest fragment. Error bars represent standard error (S.E.) and species numbers correspond with Table 2.

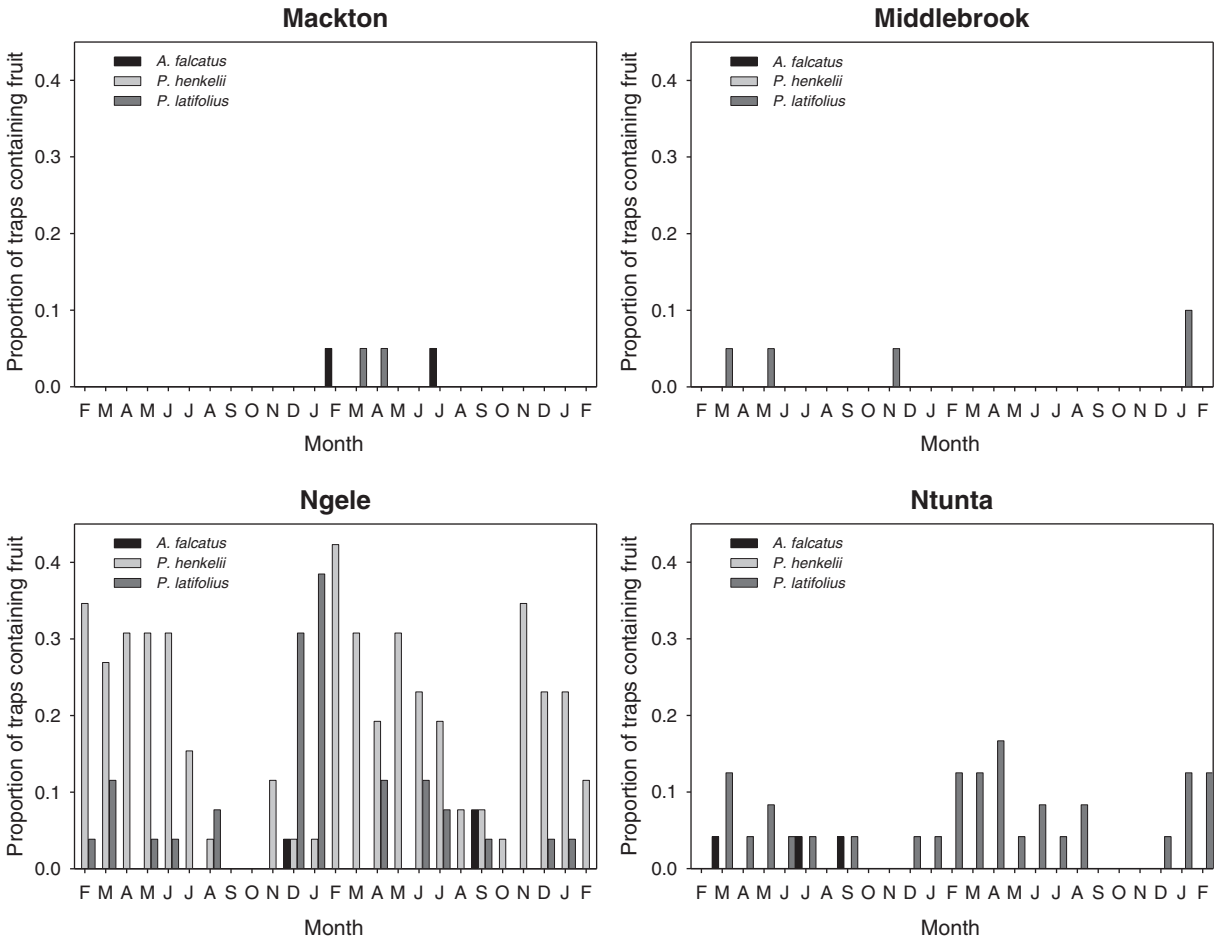

Fig. 5. Proportion of traps containing *Afrocarpus*/*Podocarpus* fruits in each forest fragment for the period February 2010 (month 1) to February 2012 (month 25).

between years have also been described for rainforests in Borneo (Brearley et al., 2007), cloud forests in Hawaii (Berlin et al., 2000), and temperate forests in America (Thompson and Willson, 1979) and Japan, with some species alternating between mast and non-mast years (Osada, 2005). As shown by these results and others (Berlin et al., 2000; Bollen and Donati, 2005; Chapman et al., 2005) fruiting patterns can vary annually and between fragments. In this study fruiting was generally higher in the second year of sampling. Differences between fragments of this study were most evident by the unpredictable and variable fruiting of podocarps and other dominant fruiting species (e.g. *P. obliquum*, *C. woodii*, *M. caffra*, *H. amoenus*, *C. edwardsii*), which differed in their fruiting contributions between fragments. The dissimilarity between results from this study and others from the same forest complex (Griffiths and Lawes, 2006; Symes et al., 2002; Wirminghaus et al., 2001c) further highlights the lack of consistent annual fruiting trends and the dissimilarity between fragments of the same forest complex. This demonstrates the requirement for long term comprehensive studies to determine phenological patterns of forest fragments. It also stresses the importance of conserving a network of forest fragments in terms of connectivity (Lawes et al., 2004; Symes et al., 2002; Wethered and Lawes, 2003) to provide a continual food source for frugivores and preserve forest ecosystem functions, such as seed dispersal (Lehouck et al., 2009).

The number of fruiting species per fragment in this study varied significantly, but overall the number of fruiting species per fragment per month was generally low and plant species varied in their fruiting patterns between fragments. These aseasonal fruiting trends with low (31%) annual fruiting, have also been highlighted in the tropical wet littoral forests of south-eastern Madagascar, which range from strongly seasonal to continuously fruiting trees (Bollen and Donati, 2005). Atlantic rain forests of southeastern Brazil also have aseasonal fruiting, however unlike results from this study, phenological patterns did not vary between sites (Morellato et al., 2000). Extended temporal fruiting was observed for some tree species in this study and others (Newton, 1988; Sun et al., 1996). Some tree species, e.g. *C. africana*, bore fruit almost consistently throughout the year, which is similar to some species from cloud forests in Hawaii (Berlin et al., 2000). Forest fragments generally differed in the composition of common fruiting species. In tropical dry evergreen forests on the Coromandel coast of India (Selwyn and Parthasarathy, 2007) and Atlantic rain forests (Morellato and Leitao-Filho, 1996) zoochorous fruits are available year round. This is due to a combination of trees of different sizes and other herbaceous species which have complementary fruiting (Morellato and Leitao-Filho, 1996). In two of the forest fragments in this study, herbaceous species were one of the species that fruited most months. In Mackton *H. amoenus* fruited for 19 months and in Ngele *C. edwardsii* fruited year round. This elucidates the value of including all fruiting species not just trees in forest phenological studies (Anderson et al., 2005; Haugaasen and Peres, 2005; Justiniano and Fredericksen, 2000; Sun et al., 1996), particularly if results are to be meaningful in terms of fruit availability to frugivores.

In South African coastal forests *Ficus burkei* fruits asynchronously produces the greatest biomass of fruits during times of fruit scarcity, making it a keystone food source for frugivores (Bleher et al., 2003). Here a keystone species refers to a species that provides an important resource to frugivores in times of food scarcity (Lambert and Marshall, 1991; Terborgh, 1986). Such trends have also been described for *Ficus* elsewhere (Justiniano and Fredericksen, 2000; Lambert and Marshall,

1991). Two *Ficus* species were found in some of the fragments from our study, but only one species was represented in the fruit traps collected in the Ntunta forest fragment. Such a low biomass contribution suggests that figs have either been lost from these fragments due to fragment reduction or are less important as a keystone species in mistbelt forests. It is important to identify the keystone species in the fragmented mistbelt forest, as the loss of these could have profound effects on frugivore communities which rely on these fruits (Bleher et al., 2003; Justiniano and Fredericksen, 2000). Forest species which fruit when there is a scarcity of other species in fruit, benefit from greater fruit removal (Burns and Wilson, 2005; Osada, 2005) and hence seed dispersal, and is characteristic of a keystone species (White, 1994). This role may be filled by *Afrocarpus*/*Podocarpus* trees, which are prominent in the forest type from this study (Moll, 1972; Pooley, 1993; Von Maltitz et al., 2003).

While, some tree species show seasonal and synchronous fruiting (Adler and Kielpinski, 2000), this was not true for *Afrocarpus*/*Podocarpus* species in this study and that of Wirminghaus et al. (2001c). It has previously been reported that these fruits are only available from June to November (Wirminghaus et al., 2001c, 2002), however results from this study show that these fruits were present more or less throughout the year in the four study fragments. Only the largest forest fragment, Ngele, yielded *P. henkelii* fruit, despite the species being recorded in Mackton. *P. henkelii* fruits were present in a great proportion of the fruit traps, almost year-round. *Afrocarpus*/*Podocarpus* fruit production was lower in the three smaller forest fragments. In southern Cape forests *A. falcatus* trees are widely scattered, occur in low densities and have low recruitment rates, while *P. latifolius* have opposite trends (Geldenhuys, 1993). Such traits could explain the lower proportion and presence of *A. falcatus* fruit observed in the various fragments. These differences and asynchronous fruiting of *Afrocarpus*/*Podocarpus* species, with few fruiting periods overlapping, highlight the need to conserve a network of these trees in all fragments to facilitate fruit availability for frugivores. This is further outlined by the presence of these species at the sites, but the lack of fruits collected for these species over the 25 month sampling period.

These *Afrocarpus*/*Podocarpus* fruiting patterns are particularly important for the endemic Cape Parrot, which relies on movement between fragments to feed on these trees (Downs, 2005; Skead, 1964, 1971; Wirminghaus et al., 2001a, 1999). In KwaZulu-Natal their inland foraging flights can reach 90 km (Skead, 1964, 1971). The presence of Cape Parrots in the Ngele forest fragment was clear from the debris of shredded *P. henkelii* husks in traps (pers. obs.). Their occurrence in forest fragments has remained largely unchanged for nearly 50 years (Downs and Hart in prep), and while annual surveys have shown that parrots are sometimes absent from certain forest fragments (Downs, 2011, 2012), this is likely due to a lack of food, as their preferred *Afrocarpus*/*Podocarpus* have mast fruiting (Herrera et al., 1994; Kelly, 1994; Koen, 1991; Silvertown, 1980; Wirminghaus et al., 2001c).

Bird diversity trends in Ngele forest did not mirror fruiting patterns observed in this study (Symes et al., 2002). Changes in bird diversity in Ngele forest are most likely due to migrant species presence in the summer months as frugivorous birds (c. 26–34 sp.) and forest specialists (c. 20–26 sp.) were present throughout the year (Symes et al., 2002). In temperate forests and others in the eastern United States, peak fruiting occurs when migratory and over-wintering bird species arrive and thus experience greater fruit removal rates (McCarty et al., 2002; Thompson and Willson, 1979). Contrastingly, evidence from Western Europe suggests that there is no link between ripening fruit and the arrival of migratory species (Guitian, 1998). The absence of a link between the number of avian dispersers and the number of fruiting trees has also been described in wet sclerophyll forests in Australia (French, 1992).

Based on trends observed in this two year study, we recommend that literature reviews not replace field sampling where possible to prevent over estimation of fruiting and masking of unpredictable fruiting patterns observed in the field. While larger fragments have been identified as important conservation areas in terms of avifaunal diversity (Symes et al., 2002), results from this study highlight the importance of smaller fragments within a network in terms of fruit supply, as plant species varied in their fruiting patterns between fragments. Continued long-term monitoring of the species composition, particularly of important fruit-bearing taxa, is therefore recommended in order to understand fluxes in fruit availability within these forest fragments. Afrotemperate forests are recognized Centres for Endemism (Van Wyk and Smith, 2001; Von Maltitz et al., 2003) and while we have highlighted the importance of these forests for Cape Parrots in particular, conservation efforts for this species would serve to benefit the many other frugivores and rare species which rely on these forest fragments. Conservation of a network of fragments of the Ngele mistbelt forest complex is therefore imperative.

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